

**First zoea of *Dissodactylus glasselli* Rioja and  
new range and host records for species of  
*Dissodactylus* (Brachyura: Pinnotheridae), with a  
discussion of host-symbiont biogeography**

Gerhard Pohle and Fernando Marques

(GP) Atlantic Reference Centre, Huntsman Marine Science Centre, Brandy Cove, St. Andrews,  
New Brunswick, E0G 2X0, Canada;

(FM) University of Toronto, Department of Zoology, 25 Harbord Street,  
Toronto, Ontario, M5S 1A1, Canada

*Abstract.* — *Dissodactylus glasselli* Rioja, is a small pinnotherid crab living as an ectosymbiont on sand dollars of the American Pacific coast. The first zoea of *D. glasselli* is described in detail and compared to that of other species within the *Dissodactylus* complex. Morphometrically the larva differs from those of the sympatric species *D. nitidus* Smith, *D. lockingtoni* Glassell, and *D. xantusi* Glassell, in the relative length of carapace spines. The zoea of *D. glasselli* most closely resembles that of *D. mellitae* (Rathbun) from the Atlantic, the two being considered trans-isthmian geminate species. A geographic range extension of *Dissodactylus lockingtoni* is reported beyond the Gulf of California to Costa Rica, where it occurs on *Mellita kanakoffi* Durham, not reported previously as a host species. The range of *Dissodactylus glasselli* is extended southward from El Salvador to Costa Rica and it is reported for the first time on the hosts *M. kanakoffi* and *Encope wetmorei* Clark. *Dissodactylus mellitae* was found on the new host *Encope aberans* Martens in the Gulf of Mexico.

---

Members of the *Dissodactylus* complex, comprising the genera *Dissodactylus* Smith, 1870 and *Clypeasterophilus* Campos & Griffith, 1990, are known as symbionts of echinoids in tropical and subtropical regions of the Americas (Schmitt et al. 1973). *Dissodactylus* is represented by four Atlantic and five Pacific species, and *Clypeasterophilus* by three and one species, respectively. Larval development is known for five Atlantic species (Pohle & Telford 1981b, 1983; Pohle 1984, Marques & Pohle 1995a, 1995b), and for Pacific species, larvae of *D. lockingtoni* Glassell, 1935, *D. xantusi* Glassell, 1936 and *D. nitidus* Smith, 1870 have been described (Pohle 1989, 1994). *Dissodactylus glasselli* overlaps geographically with the latter three sympatric species in the southern parts of the Gulf of California. The first zoea of *D. glasselli* Rioja, 1944 is described in this pa-

per and compared to that of other species within the *Dissodactylus* complex. New sand dollar hosts are reported for *Dissodactylus glasselli*, *D. lockingtoni* and *D. mellitae* (Rathbun, 1900), and the occurrence of *D. lockingtoni* has been established outside the Gulf of California.

#### Materials and Methods

During June to July 1992, first zoeae of *Dissodactylus glasselli* were obtained from a number of females collected along the Pacific coast of Costa Rica. Individual rearing techniques used to culture larvae, although successful for other species of *Dissodactylus* and *Clypeasterophilus* (Pohle & Telford 1981b, Pohle 1984, 1989; Marques & Pohle 1995a, 1995b), were not successful in this case. None of the larvae developed beyond

Table 1.—Dimensions (mm) of zoea 1 structures of *Dissodactylus glasselli* Rioja and other selected species.

Species	Spine length				Antennal length	Carapace length
	Rostral	Dorsal	Lateral	Rostrrodorsal		
<i>Dissodactylus glasselli</i>	0.35 ± 0.02 (0.32–0.37)	0.20 ± 0.02 (0.17–0.22)	0.20 ± 0.01 (0.17–0.22)	0.88 ± 0.04 (0.81–0.94)	0.10 ± 0.01 (0.09–0.10)	0.37 ± 0.01 (0.36–0.39)
<i>D. lockingtoni</i> <sup>1</sup>	0.26 ± 0.01	0.16 ± 0.01	0.14 ± 0.01	0.71 ± 0.03	0.10 ± 0.01	0.35 ± 0.01
<i>D. nitidus</i> <sup>2</sup>	0.24 ± 0.02	0.12 ± 0.01	0.12 ± 0.01	0.68 ± 0.02	0.10 ± 0.01	0.36 ± 0.01
<i>D. xantusi</i> <sup>1</sup>	0.26 ± 0.01	0.12 ± 0.01	0.13 ± 0.01	0.65 ± 0.02	0.08 ± 0.01	0.37 ± 0.01
<i>D. mellitae</i> <sup>3</sup>	0.30 ± 0.02	0.21 ± 0.01	0.16 ± 0.02	0.71 ± 0.01	0.11 ± 0.01	0.32 ± 0.01
<i>D. mellitae</i> <sup>2</sup>	0.30 ± 0.02	0.24 ± 0.01	0.20 ± 0.01	0.87 ± 0.02	0.10 ± 0.01	0.36 ± 0.01

Note: Values are given as the mean ± standard deviation, with range in parentheses for *D. glasselli*.

<sup>1</sup> From Pohle (1994); <sup>2</sup> from Pohle (1989); <sup>3</sup> from Marques & Pohle (1995b).

the first zoea. Selection of the most lively larvae, addition of antibiotics and the use of alternate food organisms, such as oyster larvae and fertilized sand dollar eggs, did not change the outcome.

Ten specimens were measured and used for morphological description. The description of setae follows Pohle & Telford (1981a), but here includes only analysis by light microscopy, using an Olympus BH-2 microscope with Nomarski Differential Interference Contrast and camera lucida. Measurements follow Pohle & Telford (1981a). Specimens of the first zoeal stage have been deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

## Results

Eggs of *Dissodactylus glasselli* were incubated by crabs for 11–13 days at 32°C. Larval morphometrics are given in Table 1.

### First Zoea (Fig. 1)

**Carapace** (Fig. 1A).—With long rostral, dorsal and lateral spines. Thickened posterior and ventral margin lacking setae. Eyes sessile. Two simple setae flanking dorsal spine. Chromatophores on each side of carapace posterior to eyes, on ventrolateral margin and base of antennules; single chromatophores located posterior to base of dorsal spine, frontally between eyes and dor-

sally on gut; abdominal somites 1–5 with paired melanophores; single chromatophore on labrum, mandibles and basipodites of first maxillipeds.

**Abdomen** (Fig. 1B).—Five somites and telson. Somite 1 naked, somites 2 and 3 with pair of dorsolateral spines; somites 2–5 with pair of simple setae dorsally.

**Telson** (Fig. 1C).—Bifurcated, with proximal minute furcal spine. Furcal shafts spinulose, except tips. Furcal arch with 3 plumodenticulate setae on either side of deep median depression. Denticulettes present in clusters on ventral and dorsal surface.

**Antennule** (Fig. 1D).—Unsegmented, smooth, conical. Terminally with 1 short and 2 long aesthetascs.

**Antenna** (Fig. 1E).—Elongate, uniramous. Tapered protopodite with 2 rows of spinules distally.

**Maxillule** (Fig. 1F).—Coxal endite bearing 4 graded plumodenticulate setae and proximal microtrichia. Basal endite with proximal microtrichia, 3 terminal plumodenticulate cuspidate setae and 2 subterminal plumodenticulate setae. Two-segmented endopodite with 4 terminal plumodenticulate setae.

**Maxilla** (Fig. 1G).—Coxal endite single-lobed, inflated, with semicircle of 4 plumose setae flanked by single proboscate (sensu Pohle & Telford 1981a) seta; scattered microtrichia. Basal endite with 4 plumodenticulate setae on either side of slight inden-

tation; microtrichia present. Endopodite unsegmented, with 3 terminal plumodenticulate setae and marginal microtrichia. Scaphognathite with 4 densely plumose setae marginally, tapering to sharp terminal process bearing microtrichia.

*Maxilliped 1* (Fig. 1H).—Coxopodite with a developing seta. Basipodite with 10 plumodenticulate setae arranged in four groups of 2, 2, 3, 3 proximally to distally. Five segmented endopodite with 2, 2, 1, 2, 4 + 1 setae proximally to distally; all plumodenticulate except single simple seta on segments 1, 2, and 5. Exopodite with 4 long natatory plumose setae.

*Maxilliped 2* (Fig. 1I).—Coxopodite naked. Basipodite with 4 plumodenticulate setae. Endopodite 2-segmented, first segment naked, distal segment with 4–5 plumodenticulate setae. Exopodite with 4 long natatory plumose setae.

*Maxilliped 3*.—Not discernible.

*Pereiopods*.—May be present as minute buds.

*Pleopods*.—Absent.

#### Range Extension and New Hosts for Species of *Dissodactylus*

*Dissodactylus lockingtoni* Glassell, 1935

*Dissodactylus lockingtoni* Glassell, 1935: 100, pl. 27, figs. 5–8, text-fig. 68 (type locality, Punta Peñasco, Sonora, Mexico).—Griffith 1987a: 401, 413, 419, figs. 8B, 9B, 11B, 13B, 14B; 1987b: 2292–2310. *D. smithi* Rioja, 1944: 149, figs. 1–6, 11–15 (type locality, Playa San Benito, Chiapas, 50 km from Tapachula, Mexico).

*Material examined*.—Puntarenas Beach, Puntarenas, Costa Rica, 9°56'N, 84°48'W; 2 Jul 1992, free-diving 0.5–1 m, sand bottom, 1 male cw 3.6 mm on *Mellita kanakoffi* Durham, 1961.—Puntarenas Beach, Puntarenas, Costa Rica, 9°56'N, 84°48'W; 18 Jul 1992, low intertidal, sand bottom, 3 females cw 5.4, 5.1 and 4.8 mm on *M. kanakoffi*.—Puntarenas Beach, Puntarenas, Costa Rica, 9°56'N, 84°48'W; 7 Aug 1992,

intertidal, low tide 0 m, sand bottom, 4 females cw 4.6, 5.0, 5.1 and 5.3 mm on *M. kanakoffi*.

*Previous range records*.—Punta Peñasco, Sonora, Mexico; “San Felipe, Gulf of California and Punta Peñasco . . . undoubtedly ranges throughout the Gulf of California” (Glassell 1935). Campo et pescador, North of San Felipe (31°04'N, 114°50'W) (Campos et al. 1992). La Choya Bay, Punta Peñasco, Sonora, Mexico (Pohle 1994).

*Previous host record*.—*Encope californica* Verrill, 1870; *E. grandis* Agassiz, 1841; *E. micropora* Agassiz, 1841; *Mellita longifissa* Michelin, 1858 (Glassell 1935).

*Remarks*.—The host *Encope californica* Verrill listed by Glassell (1935) is presently considered a junior synonym of *E. micropora* (cf. Brusca 1980) but both are probably separate species (M. Telford, in litt.).

*Dissodactylus glasselli* Rioja, 1944

*D. glasselli* Rioja, 1944: 150, fig. 7–10, 16–21 (type locality, Playa San Benito, near Tapachula, Chiapas, Mexico).—Griffith 1987a: 413, 420, figs. 8H, 9H, 11H, 13H; 1987b: 2292–2310.

*Material examined*.—Manuel Antonio National Park, Manuel Antonio, Costa Rica, 9°06'N, 84°11'W; 20 June 1992, SCUBA diving 1.5–3 m, sand bottom, 3 males cw 3.6, 3.6 and 3.8 mm, 3 females cw 3.3, 4.2 and 4.2 mm on *Mellita kanakoffi* and *Encope wetmorei* Clark, 1946.—Brasilito Beach, Guanacastes, Costa Rica, 10°25'N, 85°47'W; 22 Jun 1992, SCUBA diving 1–3 m, sand bottom, 4 males cw 2.4, 3.2, 3.9 and 4.0 mm, 2 females cw 3.4 and 4.6 mm on *Encope micropora*.—Brasilito Beach, Guanacastes, Costa Rica, 10°25'N, 85°47'W; 13 Jul 1992, SCUBA diving 1–3 m, sand bottom, 3 females cw 3.0, 3.8 and 5.0 mm on *Encope micropora*.

*Previous range records*.—Playa San Benito, near Tapachula, Chiapas, Mexico (Glassell 1935). Puerto el Triunfo, El Salvador (Griffith 1987a).

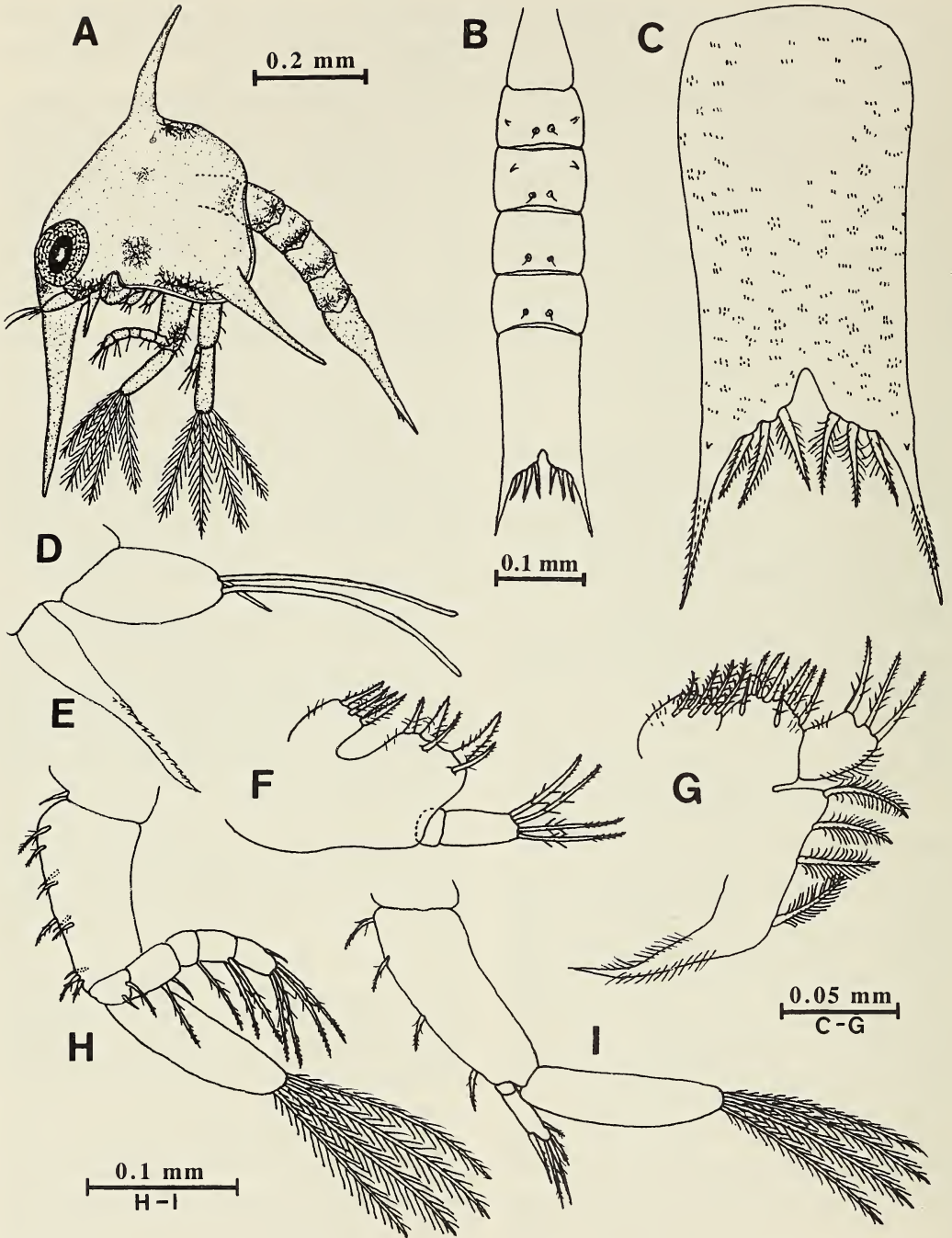


Fig. 1. First zoea of *Dissodactylus glasselli* Rioja, 1944. A, lateral view; B, dorsal view of abdomen; C, telson; D, antennule; E, antenna; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2.

*Previous host record.*—*Mellita longifissa* Michelin (Rioja 1944).

*Remarks.*—The specimens collected at Brasilito Beach were sharing the same host with *Dissodactylus nitidus* Smith, 1870.

*Dissodactylus mellitae* (Rathbun, 1900)

*Echinophilus mellitae* Rathbun, 1900: 590 (type locality, Pensacola, Florida).

*D. mellitae* Rathbun, 1901: 22.—Griffith 1987a: 413, 420, figs. 8I, 9I, 11I, 13I, 14G; 1987b: 2292–2310.

*Material examined.*—East beach, Desoto Fort, St. Petersburg, Florida, Gulf of Mexico; 20 Aug 1992, free-diving 2–3.5 m, sand bottom, 2 females cw 4.0 and 4.2 mm on *Encope aberans* Martens, 1867.

*Previous host records.*—*Echinarachnius parma* (Lamarck, 1816), *Mellita quinquiesperforata* (Leske, 1778) (cf. Rathbun 1901, Telford 1982, Bell & Stancyk 1983, Bell 1984, 1988); *Mellita tenuis* Clark, 1940 (Marques & Pohle 1995b); *Encope michelini* Agassiz, 1841; and *Clypeaster subdepressus* (Gray, 1825) (cf. Williams et al. 1968).

#### Comparison of *D. glasselli* Larvae with those of Other Species of the *Dissodactylus* Complex

Meristic characteristics of the first zoea of *Dissodactylus glasselli* are identical to other species of this genus. There are, however, some morphometric differences between *D. glasselli* and the three other sympatric Pacific species, *D. nitidus* Smith, 1870, *D. lockingtoni* Glassell, 1935 and *D. xantusi* Glassell, 1936 (Pohle 1989, 1994). While the first zoea of the latter three are almost indistinguishable, *Dissodactylus glasselli* differs by significantly longer ( $P < 0.01$ ) carapace spines (Table 1). Carapace length, however, overlaps with the other Pacific species. The closely related *Clypeasterophilus ususfructus* (Griffith, 1987a), which has recently been removed from *Dissodactylus* (Campos & Griffith 1990), is also known

from near the mouth of the Gulf of California (Hendrickx 1990). Although larvae of *C. ususfructus* are unknown, it is expected that the zoeae will differ from *Dissodactylus* by the absence of dorsolateral spines on abdominal somite 3, as known for *Clypeasterophilus stebbingi* (Rathbun, 1918) and *C. rugatus* (Bouvier, 1917) (cf. Marques & Pohle 1995a, Pohle 1984).

Larvae of *D. glasselli* resemble most closely those of *D. mellitae* from the Atlantic (Marques & Pohle 1995b), *D. glasselli* differing only by the relatively longer rostral and lateral spines (Table 1). The similarity between these two species supports the conclusion by Griffith (1987b), based on an analysis of adult synapomorphies, that these are twin, or geminate, species. Trans-isthmian pairs of closely related species have been described for many taxa, including about 45% of extant decapods of Panama (Abele 1976). Under vicariant biogeographic theory (Rosen 1975), these species evolved by allopatric speciation, following the closing of the Panama seaway. The relatively recent separation accounts for the similarity of eastern Pacific and Caribbean species, such as that seen between *Dissodactylus mellitae* and *D. glasselli*.

#### Host-symbiont Biogeography

*Dissodactylus lockingtoni* has never before been reported outside the Gulf of California and thus its occurrence in Costa Rica represents about a 20° southward extension. The hosts *Mellita longifissa* and *Encope micropora* extend further south to Panama and Chile, respectively (Ghiold 1988). Thus, the geographic range of *Dissodactylus lockingtoni* may also extend beyond Costa Rica.

*Dissodactylus glasselli* was only known from its type locality in Mexico until Griffith (1987a) discovered a specimen amongst a lot in the Smithsonian collection identified as *D. lockingtoni* from El Salvador. The record in Costa Rica represents a 3° southward extension. The hosts *Mellita longifissa* and *M. kanakoffi* both extend further south to

at least Panama (Harold & Telford 1990), indicating that *D. glasselli* may also be found there.

In terms of host specificity, *Dissodactylus mellitae* is the most generalist species within the *Dissodactylus* complex, inhabiting echinoids from three distinct clypeasteroid families. Other Atlantic species of *Dissodactylus*, except for *D. primitivus* and *D. schmitti* which live on heart urchins (Griffith 1987a), can be found on mellitid sand dollars and two species of *Clypeaster*. In contrast, the Pacific species of this genus have never been found on any of the *Clypeaster* species occurring in the area.

In contrast to *Dissodactylus*, Atlantic and Pacific species of *Clypeasterophilus* are found exclusively on *Clypeaster* (Griffith 1987a, Hendrickx 1990). The following evidence suggests that species of *Clypeasterophilus* are also more host dependent than those of *Dissodactylus*: 1) an analysis of gut contents of *Clypeasterophilus rugatus* and three species of *Dissodactylus* by Telford (1982) showed that only *C. rugatus* fed exclusively on host tissue, whereas *D. primitivus* took no more than about half of its food from the spatangoid host; 2) larvae of *Clypeasterophilus* (Pohle 1984, Marques & Pohle 1995a) could not complete larval development in absence of a host, whereas *Dissodactylus primitivus* could (Pohle & Telford 1983).

#### Acknowledgments

This work was supported through research grant A2313 to G. Pohle, from the Natural Sciences and Engineering Research Council, Canada. Dr. A. Dittel is thanked for arranging the use of facilities at the Centro de Investigacion de Ciencias del Mar (CIMAR), Universidad Nacional, Costa Rica, and for providing advice and equipment. We also thank technical support personnel at CIMAR. Dr. M. Telford from the Department of Zoology at the University of Toronto kindly identified the echinoid hosts. Drs. M. Telford and H. Griffith also reviewed the manuscript.

#### Literature Cited

- Abele, L. G. 1976. Comparative species composition and relative abundance of decapod crustaceans in marine habitats of Panama.—*Marine Biology* 38:263–278.
- Agassiz, L. 1841. Des Scutelles. Monographies des Echinodermes Vivans et Fossiles. Monograph 2:1–151.
- Bell, J. L. 1984. Changing residence: dynamics of the symbiotic relationship between *Dissodactylus mellitae* Rathbun (Pinnotheridae) and *Mellita quinquesperforata* (Leske) (Echinodermata).—*Journal of Experimental Marine Biology and Ecology* 82:101–115.
- . 1988. Distribution and abundance of *Dissodactylus mellitae* Rathbun (Pinnotheridae) on *Mellita quinquesperforata* (Leske) (Echinodermata).—*Journal of Experimental Marine Biology and Ecology* 117:93–114.
- , & S. E. Stancyk. 1983. Population dynamics and reproduction of *Dissodactylus mellitae* (Brachyura: Pinnotheridae) on its sand dollar host *Mellita quinquesperforata* (Echinodermata).—*Marine Ecology Progress Series* 13:141–149.
- Bouvier, M. E.-L. 1917. Gonoplacides et Pinnotherides nouveaux recueillis au cours des campagnes americaines du "Hassler" et du "Blake".—*Bulletin du Muséum national d'Histoire naturelle*, Paris 23:391–398.
- Brusca, R. C. 1980. Common intertidal invertebrates of the Gulf of California. The University of Arizona Press, Tucson, 513 pp.
- Campos, E., & H. Griffith. 1990. *Clypeasterophilus*, a new genus to receive the small-palped species of the *Dissodactylus* complex (Brachyura: Pinnotheridae).—*Journal of Crustacean Biology* 10: 550–553.
- , A. R. de Campos, & J. Ramirez. 1992. Remarks on distribution and hosts for symbiotic crustaceans of the Mexican Pacific (Decapoda and Isopoda).—*Proceedings of the Biological Society of Washington* 105:753–759.
- Clark, A. H. 1946. Echinoderms from the Pearl Islands, Bay of Panama, with a revision of the Pacific species of the genus *Encope*.—*Smithsonian Miscellaneous Contributions* 106 (5):1–11, 4 pls.
- Clark, H. L. 1940. Revision of the keyhole urchins (*Mellita*).—*Proceedings of the United States National Museum* 89:435–444.
- Durham, J. W. 1961. The echinoid *Mellita* in the Pacific coast Cenozoic.—*Los Angeles County Museum Contributions in Science* 48:1–12.
- Ghiold, J. 1988. Species distributions of irregular echinoids.—*Biological Oceanography* 6:79–162.
- Glassell, S. A. 1935. New or little known crabs from the Pacific coast of northern Mexico.—*Trans-*

- actions of the San Diego Society of Natural History 8:91–106.
- . 1936. New porcellanids and pinnotherids from tropical North American waters.—Transactions of the San Diego Society of Natural History 8:277–304.
- Gray, J. E. 1825. An attempt to divide the Echinida, or sea eggs, into natural families.—Annals of Philosophy 26:423–431.
- Griffith, H. 1987a. Taxonomy of the genus *Dissodactylus* (Crustacea: Brachyura: Pinnotheridae) with descriptions of three new species.—Bulletin of Marine Science 40:397–422.
- . 1987b. Phylogenetic relationships in the genus *Dissodactylus* Smith, 1870 (Crustacea: Brachyura: Pinnotheridae).—Canadian Journal of Zoology 65:2292–2310.
- Harold, A. S., & M. Telford. 1990. Systematics, phylogeny and biogeography of the genus *Mellita* (Echinoidea: Clypeasteroidea).—Journal of Natural History 24:987–1026.
- Hendrickx, M. E. 1990. Range extension and host record for *Dissodactylus ususfructus* Griffith, 1987 (Crustacea: Brachyura: Pinnotheridae).—Proceedings of the Biological Society of Washington 103:106–107.
- Lamarck, J. B. 1816. Histoire naturelle des animaux sans vertèbres. III. Verdrière, Paris, 130 pp.
- Leske, N. G. 1778. Additamenta ad Jacob Theodori Klein naturalem dispositionem echinodermatum et lucubratiunculam de aculeis echinorum marinorum. Upsala, 216 pp.
- Marques, F., & G. Pohle. 1995a. The complete larval development of *Clypeasterophilus stebbingi* (Decapoda: Brachyura: Pinnotheridae) and a comparison with other species within the *Dissodactylus* complex.—Bulletin of Marine Science (in press).
- , & ———. 1995b. Laboratory-reared larval stages of *Dissodactylus mellitae* (Decapoda: Brachyura: Pinnotheridae) and developmental patterns within the *Dissodactylus* complex.—Canadian Journal of Zoology (in press).
- Martens, E. von. 1867. Über ostasiatische Echinodermen (Fortsetzung).—Archiv für Naturforschung. Jahrgang XXXIII (1):106–119, 3 pls.
- Michelin, M. H. 1858. Du genre *Mellita* Famille des Clypeasteroïdes.—Revue et Magasin de Zoologie 8:2–7.
- Pohle, G. 1984. Larval development of *Dissodactylus rugatus* Bouvier, 1917 (= *D. calmani* Rathbun, 1918) (Brachyura: Pinnotheridae) reared under laboratory conditions.—Journal of Crustacean Biology 4:572–588.
- . 1989. Development and morphology of laboratory-reared larvae of *Dissodactylus nitidus* Smith, 1840 (Decapoda: Brachyura), with a discussion of phylogenetic aspects in the Pinnotheridae.—Journal of Crustacean Biology 9:278–296.
- . 1994. *Dissodactylus xantusi* and *D. lockingtoni* (Decapoda: Brachyura: Pinnotheridae): larval development of two sympatric Pacific species.—Canadian Journal of Zoology 72:575–590.
- , & M. Telford. 1981a. Morphology and classification of decapod crustacean larval setae: a scanning electron microscope study of *Dissodactylus crinitichelis* Moreira, 1901 (Brachyura: Pinnotheridae).—Bulletin of Marine Science 31:736–752.
- , & ———. 1981b. The larval development of *Dissodactylus crinitichelis* Moreira, 1901 (Brachyura: Pinnotheridae) in laboratory culture.—Bulletin of Marine Science 31:753–773.
- , & ———. 1983. The larval development of *Dissodactylus primitivus* Bouvier 1917 (Brachyura: Pinnotheridae) reared in the laboratory.—Bulletin of Marine Science 31:753–773.
- Rathbun, M. J. 1900. Synopsis of North American invertebrates. XI. The catometopous or grapsoid crabs of North America.—American Naturalist 34:583–591.
- . 1901. The Brachyura and Macrura of Porto Rico.—Bulletin of the United States Fish Commission 20:1–127.
- . 1918. The grapsoid crabs of America.—United States National Museum Bulletin 97:1–461, 161 pls.
- Rioja, E. 1944. Estudios carcinológicos XVI. Observaciones sobre algunas especies de cangrejos del género *Dissodactylus* Smith (Braquiros, Pinnotheridos) de las costas Mexicanas del Pacifico.—Anales del Instituto de Biología de México 15:147–160.
- Rosen, D. E. 1975. A vicariance model of Caribbean biogeography.—Systematic Zoology 24:431–464.
- Schmitt, W. L., J. C. McCain, & E. S. Davidson. 1973. Decapoda I. Brachyura I. Family Pinnotheridae. In H. E. Gruner & L. B. Holthuis, eds., *Crustaceorum Catalogus* III. W. Junk B. V., Den Haag, The Netherlands, 160 pp.
- Smith, S. I. 1870. Notes on American Crustacea. No. 1. Ocypodoidea.—Transactions of the Connecticut Academy of Arts and Science 2:113–176, pls 2–5.
- Telford, M. 1982. Echinoderm spine structure, feeding and host relationships of four species of *Dissodactylus* (Brachyura: Pinnotheridae).—Bulletin of Marine Science 32:584–594.
- Verrill, A. E. 1870. Description of echinoderms and corals from the Gulf of California.—American Journal of Science 49:93–100.
- Williams, A. B., I. R. McClosky, & I. E. Gray. 1968. New records of brachyuran decapod crustaceans from the continental shelf off North Carolina, U.S.A.—Crustaceana 15:41–66.